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The influence of social experience on the development and fixation of the form of displays in the black-headed gull

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Abstract. Previous studies have shown that the form of the species-specific displays in young black-headed gulls, *Larus ridibundus*, gradually emerges, via incomplete patterns, to the final complete adult form. These incomplete patterns were almost exclusively performed during social interactions with conspecifics. This study investigated the role of experience, especially social experience, gained during the performance of incomplete display, and of imitation in the development of the complete form. The possible influence of these factors on the frequency and (stability of) form of display was manipulated by rearing chicks in different social contexts, after which the birds were re-housed in large groups of at least 10 birds. Stereotyped deviations in postures and calls were found in birds reared in groups of a few birds and their possible cause is discussed. No evidence for an influence of imitation was found. Although some birds reared in social deprivation developed the normal complete displays, the majority of the birds in this group showed a retardation in display development; after the birds were re-housed in large groups they made up for this by frequently performing incomplete display. This suggests that (social) experience, gained by the performance of these incomplete forms, fulfils a function in the development of complete display. However, display retardation is associated with a retardation in testosterone production, probably caused by lack of social stimulation. This suggests that incomplete forms of display may be epiphenomena of low levels of testosterone. Such levels are probably normally present in young gulls, and may gradually rise in ontogeny as the consequence of the many aggressive interactions these birds have on the territory. This may lead to the gradual emergence of complete display, after which these motor patterns become fixed in form.

To investigate the mechanisms by which stereotyped motor patterns develop, the ontogeny of the species-specific displays of the black-headed gull, *Larus ridibundus*, was studied. Previously (Groothuis 1989a, b; Groothuis & van Mulekom 1991), it was found that: (1) the period it takes for the adult form to emerge is relatively long, compared with the developmental period of locomotory patterns; (2) the displays gradually change in form during ontogeny, from incomplete or transitional forms to the complete adult form; (3) young gulls perform incomplete displays almost exclusively during agonistic interactions with conspecifics; (4) the change in form of display behaviour is related to changes in motivational factors for aggressive and fear behaviour; and (5) social experience influences the development of motivational factors for aggressive and fear behaviour. These findings suggest that social experience, gained during the performance of incomplete display, influences the development in form of the complete species-

specific display. I shall consider four different, not necessarily mutually exclusive, ways that could bring this about. (1) A young bird may shape its display on the basis of reactions of opponents to that display. Conspecifics may react differently to alternative forms of a display, and this may 'teach' the displaying bird to use the most effective form of a species-specific posture or call. (2) A young bird may incorporate into its own motor output through imitation (observational learning) the form of display performed by other birds. (3) Social interactions may stimulate the development of motivational factors for agonistic behaviour, such as hormonal factors needed for the complete display to occur. (4) Social interactions may stimulate the performance of display and this may lead to an improvement in the motor output, not by incorporating social experience, but merely on the basis of practising motor abilities. This may involve matching the actual motor performance on the basis of proprioceptive feedback against some sort

of template that holds information about the species-specific form of the display.

The latter two procedures influence only the speed of development, whereas the first two may also influence the development of the form itself. In this study I test these four suggestions by investigating the effect of various forms of manipulation of social interactions on the development and fixation of the form of displays in young gulls.

MATERIALS AND METHODS

Experimental Groups

Black-headed gull chicks were reared and observed in one of five different conditions in which they were deprived of social interactions. I tested the effect of rearing conditions on the development of display behaviour by placing all birds in large groups of at least 10 conspecifics after they had reached the age of 10–12 months. The five conditions were designed for the following reasons.

(1) To exclude entirely the opportunity for birds to shape their display on the basis of social interactions and imitation, 20 birds were reared individually in visual isolation from other birds. I expected these birds hardly ever to practise their motor abilities on the basis of proprioceptive feedback, owing to the lack of social stimulation.

(2) To investigate the stability of already established motor patterns, eight birds were visually isolated after the complete display had developed. These birds had been reared in large groups of at least nine conspecifics, in which they had had many agonistic interactions, until the age of 4–7 months. At that time they had frequently performed complete displays.

(3) Additional information about the possibility of imitation was obtained by rearing four birds without conspecifics in a small group of gulls of another species, the common gull, *Larus canus*, and the little gull, *Larus minutus*. In spite of similarities between displays of these species and those of the black-headed gull, there are consistent differences between them in major elements of postures and calls (Moynihan 1955; Weidman 1955). Two of the four experimental birds were reared from the age of 2 weeks in groups of five common gulls of the same age. The third was reared from the age of 1 week in a group of three little gulls of the same age. The fourth was reared from hatching by a pair of adult common gulls, housed together with three other adults of that species.

(4) The influence of social reactions on the development of display was tested by rearing birds with abnormal social interactions. Birds in abnormally small groups were expected to have abnormal social interactions, because they were very restricted in the diversity of reactions they received from conspecifics to their display performance. Therefore, 20 birds were reared in small groups of two to four individuals of the same age, in visual isolation from other groups.

(5) As controls for the other rearing conditions I used 18 young gulls reared from the age of 0–5 days by their own or by foster parents in a semi-natural situation: a large aviary with several breeding pairs.

Rearing Conditions

All experimental birds were collected in the field at less than 5 days after hatching. Young chicks were fed a mixture of water, dried insects, yeast and trout pellets. They were stimulated to eat by presenting them with food in front of their bills on the end of a small stick. Older gulls were fed dry pellets and had a bathing pool in their cage; the water was replenished almost daily. The birds were kept in indoor cages until the age of 4–5 weeks; then they were re-housed in larger outdoor cages, mostly at densities of at least one bird per m².

Observations and Tests

All birds in all conditions were observed frequently during the first 8 months of age. During the 9th and 10th months, each bird was observed for at least 10 h. Between the ages of 10 and 12 months, all experimental birds were placed in large groups of conspecifics, containing at least 10 birds ranging in age from 1 to 4 years. These groups were housed in aviaries of 10 × 6 m, with several food containers and one bathing pool. Control birds, reared in these groups, were removed from their original group to other large groups of at least 10 birds during testing. The behaviour of the birds after re-housing was monitored for 1–3 years thereafter.

Display behaviour and vocalizations of all birds were recorded on a VHS video recorder, type JVC HR D725 EB; vocalizations were analysed with a Uniscan I type 4500 Spectrum Analyser.

Differences in the development of display between individuals in the same rearing condition were studied in relation to sex and individual differences in the production of testosterone. Sex was

determined on the basis of the size of bill and head (van Rhijn 1985) and in case of doubt, by autopsy. Testosterone production was determined on the basis of the brown mask. The development of this mask, which is repeated each spring, is known to be dependent on testosterone, as shown by castration experiments (van Oordt & Junge 1933), and experiments in which young gulls were implanted with pellets of testosterone propionate (unpublished data). The stage of development of the brown mask was scored at the time the birds were re-housed in large groups; at this time this development was at its maximum. It was scored in six stages, ranging from 1 (no more brown feathers on the head than black-headed gulls have during winter) to 6 (fully developed brown mask).

The Displays

Most data were collected on the development of the oblique display. Usually, an adult performs two forms of this erect posture: the 'normal oblique' in which the neck is held obliquely and the bill either horizontally or inclined upwards, and the 'straight up' in which the neck is held vertically and the bill is above the horizontal (Fig. 1a, b). In both postures the carpal joints are almost always raised. The display lasts 2–4 s. It is always accompanied by the long-call: a series of harsh notes in rapid succession, in which the first notes last considerably longer than the final ones (Fig. 2e, f).

Additional data were collected on three other displays.

(1) The 'forward' is a posture in which the head is held in front of the body while the neck is somewhat extended and the carpal joints are raised. The so-called 'low-up' is considered a more extreme form of the normal forward (Fig. 1c, d). Both forms are often performed in sequence with the oblique, and accompanied by the final notes of the long-call.

(2) 'Choking' is a posture in which the bill is held down and the body is tilted towards the ground. The carpal joints are raised and the bird often performs rapid vertical head movements with a small amplitude (Fig. 1f). During this posture the bird always produces the typical choking-call, a series of short stifled notes in rapid succession.

(3) The 'upright' is a pronounced erect posture in which the neck is held vertically and the bill often kept horizontally (Fig. 1e). It is performed without vocalization.

The form of these four displays has been quantitatively described by van Rhijn (1981), based on

field observations of adult gulls, and by myself (Groothuis 1989a), based on observations of gulls of several age classes, reared in large groups of at least 10 birds. These data will serve as reference for the results obtained for the experimental birds in this study.

The outcome of the development of display was classified in four mutually exclusive categories.

(1) In 'normal' display no deviations in the form of the postures or calls performed could be detected when they were compared with the reference data just mentioned.

(2) 'Deviating' display consisted of pronounced display with a normal duration, but with some stereotyped element in the posture or structure of the call being consistently different from normal display.

(3) 'Fragmentary' display consisted of less pronounced postures with a short duration (approximately less than 1 s) and often variable in form. These displays looked quite similar in form to incomplete display, typical of young gulls.

(4) 'None' means that the bird did not perform any display of a particular type during the observation periods.

By the time the birds were approximately 10 months old, just before they were re-housed in large groups, for each bird, the outcome of the development of the oblique was classified in one of the four display categories, given above. None of the birds frequently performed more than one category of this display.

Fixation of displays was tested in the re-housing experiments. For each bird, reared in a small group or in isolation from early on, the form of its display was scored in one of the four categories, in four successive periods, ranging from just before re-housing to at least 1 year after re-housing.

RESULTS

Abnormal Rearing Conditions

Differences between conditions in oblique display just before re-housing were tested with the Fisher exact test. As expected, all birds reared by their (foster) parents in the large control groups showed normal oblique display (Table I). Forty per cent of the birds reared in isolation from early on were also able to perform normal oblique postures and calls. No stereotyped deviations were found in this condition. However, 60% of these isolates showed no display at all or only fragmentary display. This is significantly more than in the control

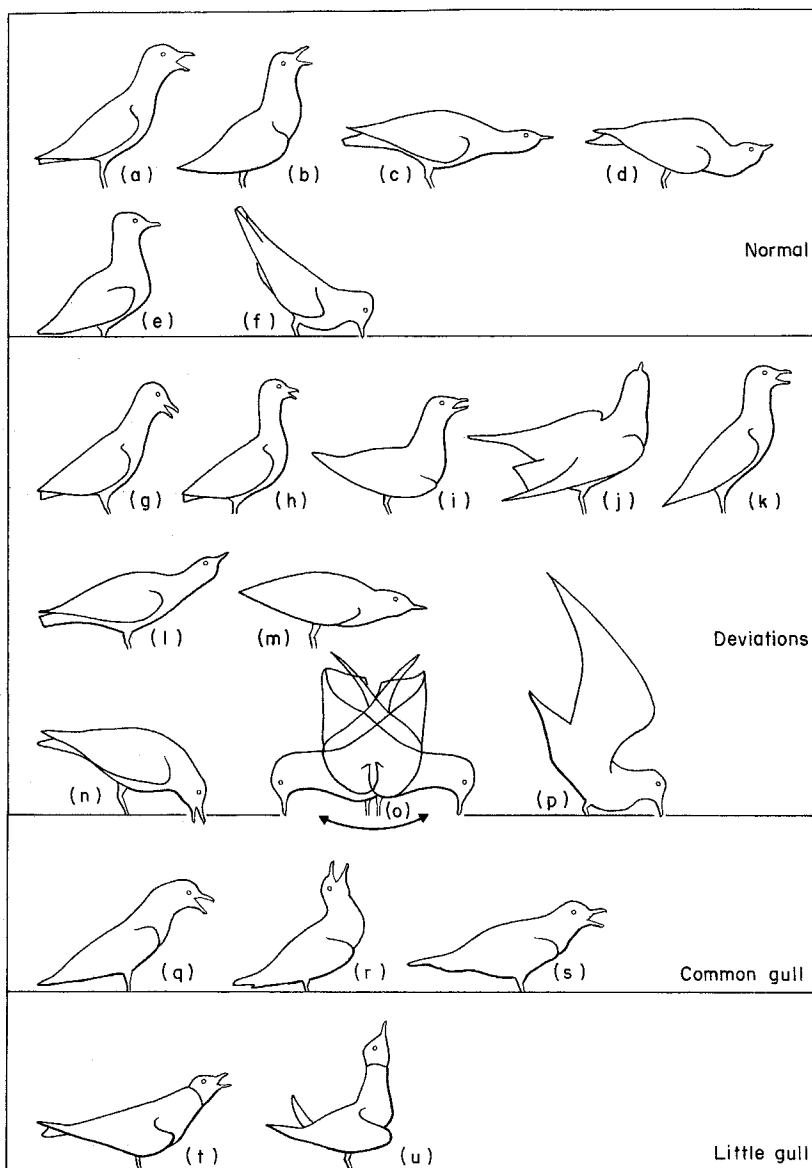


Figure 1. Normal forms of species-specific displays in black-headed gulls, common gulls and little gulls, and examples of stereotyped deviations in form of the displays of black-headed gulls, reared under abnormal social conditions. (a–f) Normal black-headed gull display: (a) common oblique; (b) extreme oblique or straight up; (c) common forward; (d) extreme forward or low-up; (e) upright; (f) choking. (g–k) Stereotyped deviations in form of oblique display; (l) abnormal forward; (m) incomplete forward; (n–p) deviations in form of choking display. See text. (q–s) Oblique ceremony in common gulls. (t–u) Oblique ceremony (horizontal and vertical) in little gulls.

group ($P < 0.01$). Thus isolation can indeed affect the emergence of complete display.

In contrast to the birds reared in isolation from early on, most birds isolated after they had developed normal oblique display continued to show

these normal forms of the oblique after the end of the isolation period (Table I). Probably because of the small number of these birds, the difference in display performance between both types of isolation was not statistically significant ($P = 0.1$). However,

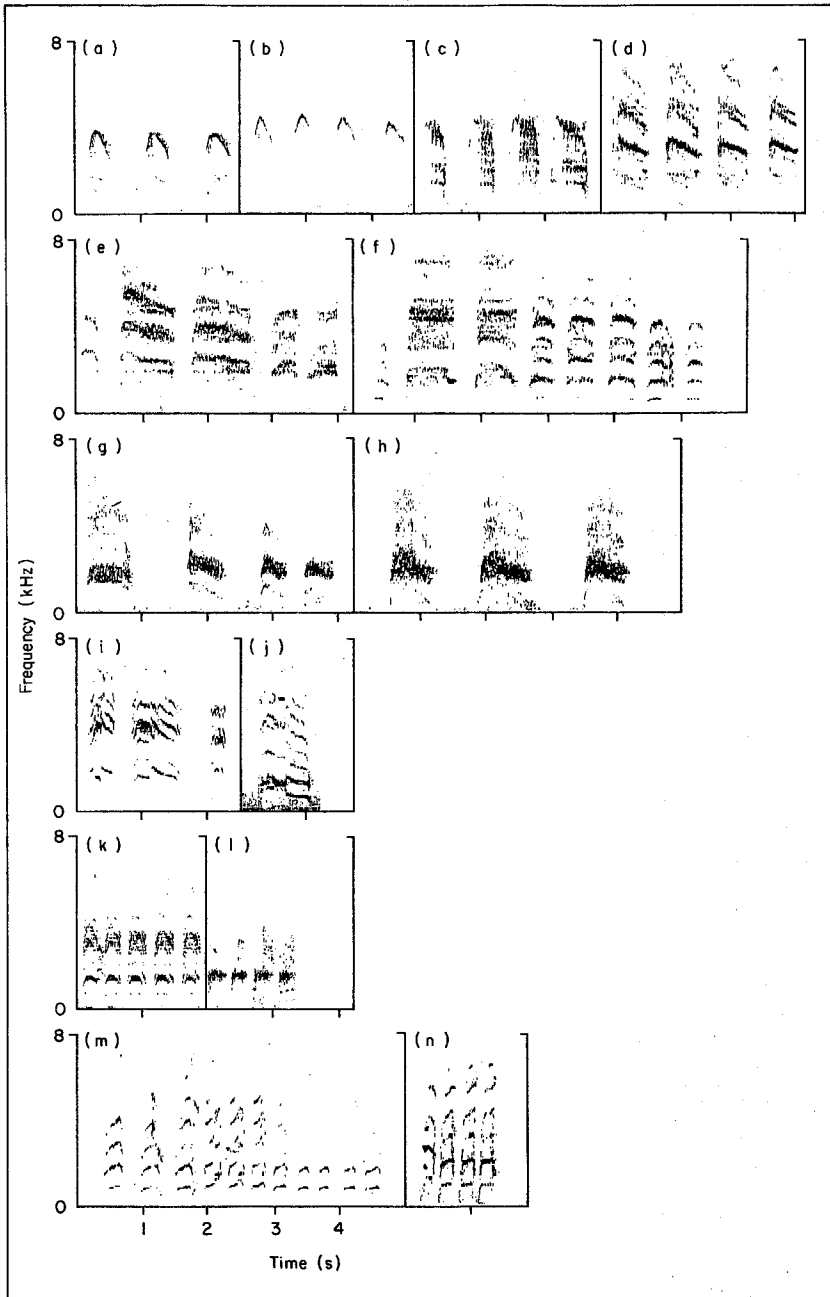


Figure 2. Sonograms of normal and abnormal calls in black-headed gulls, reared in different social situations. (a, b) Normal begging calls; (c, d) abnormal begging calls; (e, f) normal long-call; (g) normal hoarse long-call typical for juvenile gulls; (h) hoarse long-call, typical for fragmentary oblique display; (i, k, m) deviating long-calls; (j, l, n) possible developmental origins of deviating long-calls: choking-call (l, n) and mew-call (j). See text for further details.

Table 1. Percentage of 10-month-old gulls, reared in different conditions, showing various types of development of oblique display

Type of display	Rearing condition				
	Controls	Isolation	Isolation after 4 months	Small group	With other species
None	0	35	0	0	25
Fragmentary	0	25	25	20	0
Stereotyped deviations	0	0	0	25	50
Normal	100	40	75	55	25
N	18	20	8	20	4

while the early-isolated group did differ from the control group (see above), the late-isolated group did not differ statistically from the control group ($P=0.9$). So the results indicate that the display that did develop was relatively stable in form.

Approximately half of the birds reared in small groups developed normal display (55%), as was the case for birds reared in isolation (40%). But in the small groups 25% showed stereotyped deviations of the normal form. This is significantly more than in the group of early-isolated birds ($P<0.03$). Stereotyped deviations were also found in two of the four birds reared in small groups without conspecifics but with another species. Only the one bird that was reared by adult common gulls showed normal display. Thus experience in small groups in particular seems to induce stereotyped deviations in display.

Although displays other than the oblique were less frequently performed, two birds, both reared in small groups, showed deviations in the forward display. Two birds, reared with common gulls, showed only incomplete forms, and one isolated bird only the extreme low-up type of this posture. One isolated bird performed abnormal choking.

More details of abnormal forms of display are presented below.

Changes in Display after Re-housing

Birds showing normal oblique display just before re-housing still performed normal oblique postures and long-calls in the three successive periods afterwards (Fig. 3): none of these birds shifted its display to one of the other three categories. This is in line with results obtained from control birds, reared normally in large groups and re-housed at approximately the same time as the experimental birds. These controls, showing normal display in their

original group, still performed normal postures and calls after replacement.

Stereotyped deviations were relatively stable in form too. Almost all birds showing deviating obliques in their original rearing condition still performed these abnormalities 1 week after re-housing; only one bird changed its display to fragmentary postures (Fig. 3a). Even 10 weeks after being re-housed, five of these seven birds still frequently performed these deviations. Two birds shifted to normal display, but in one of these gulls the old deviation could sometimes still be observed (Fig. 3b). After more than 1 year, all birds usually performed normal forms of oblique postures and calls. However, the old deviations could still be seen or heard (Fig. 3c). This was especially so when the birds were involved in highly aggressive interactions, when competing for food or water, or when defending eggs or young against intruders on the territory.

Birds performing fragmentary display before re-housing changed their display more frequently during the first 10 weeks after re-housing than the birds with deviating obliques ($P=0.024$). Only one of the former continued to perform fragmentary display frequently at the end of this period. The others shifted mostly to normal forms, but also to deviating forms of display (Fig. 3b). Again, after more than 1 year after re-housing, almost all birds showed normal display, although the old deviations sometimes returned into the repertoire (Fig. 3c), especially during aggressive interactions.

All birds that had not shown any oblique display before re-housing performed fragmentary display immediately afterwards (Fig. 3a). They eventually shifted their displays in a way similar to birds showing fragmentary display before re-housing (Fig. 3b, c). Thus, birds that performed no display

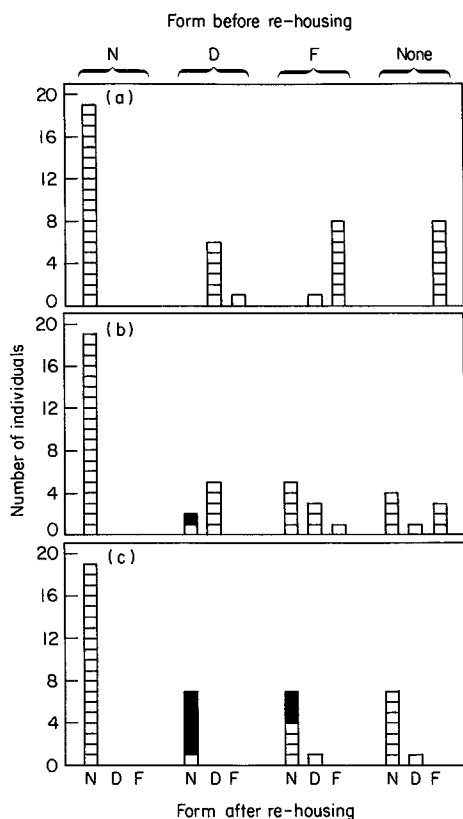


Figure 3. Shift in form of oblique display of young gulls reared under abnormal social conditions in several periods after they were re-housed in groups of at least 10 conspecifics in relation to the display performed before they were re-housed. Each square is one individual. ■: deviation in display not completely disappeared. (a) After 1 week; (b) after 10 weeks; (c) after more than 1 year. N: normal complete display; D: stereotyped deviation in form of oblique display; F: fragmentary oblique display; None: no display performed at all. For definitions see text.

before re-housing completed their development via fragmentary display. Apparently they could not omit these motor patterns, which are rather similar to incomplete forms of display, typical of young birds. This suggests that (social) experience, gained during the performance of incomplete display, is a necessary step in the development of the complete form.

Deviating and Fragmentary Display

When stereotyped deviations occurred in a particular type of display, they were present almost every time the bird performed that type of display (Table II). This demonstrates that deviations in form became stereotyped parts of the behaviour

patterns. In most cases, however, the percentage of postures in which abnormal elements occurred decreased considerably after the birds had been housed in the large group for 2–3 years (Table II).

At least some of these deviations can be considered in relation to elements of displays typical of the incomplete displays of young black-headed gulls (Table II). For example, obliques in which the bill points down are seldom seen in normal adult gulls, but are often seen in gulls younger than 6 weeks; and whereas the normal long-call has its developmental origin in the choking vocalization, two birds still performed these choking notes during the oblique. Thus, elements that are typical of the display of young birds became stereotyped characteristics of the display of adult gulls deprived of normal social interactions.

Although in some cases the same abnormality was found in displays of different birds, such birds were never reared in the same group. Therefore, no evidence was obtained for the occurrence of 'cultural transmission' of stereotyped abnormalities in the form of display.

Two birds reared with common gulls showed deviating display. However, they did not show species-specific elements of display of this related species (Fig. 1q–s), e.g. the extremely upward pointing bill or head-tossing in the oblique. One bird had its body strongly tilted upwards during the oblique, together with a vertically erect neck. This was possibly evoked by the larger size of its companions. The other bird showed one long note only in its long-call. This bird was rather shy. It often ended its oblique abruptly when a common gull reacted to its display, and this became a stereotyped element in its display later on, after re-housing, when the original shyness had disappeared. Also, the bird reared with little gulls of the same age did not copy elements of species-specific display of this species. Its deviation consisted of abnormal notes in the long-call, typical of young gulls, without any resemblance to the long-call of the little gull. Moreover, the black-headed gull performed the forward display typical of its own species and only rarely seen in the little gull. It did not copy the vertical posture, typical of the species with which it was reared. So none of the birds individually reared with birds of another species copied elements of display typical for these species in their own display.

The experimental birds did not only show deviations in their agonistic display. Two isolated birds performed abnormal begging calls during the

Table II. Deviations in form of displays of gulls reared in isolation, in small groups or with another species and then re-housed in large groups

Display	Deviations appearing before or after re-housing	Figure	Rearing condition	Frequency of deviations						Remarks
				Just before/after re-housing		2-3 years after re-housing		Adults reared in large groups		
				%	N	%	N	%	N	
Before birds were re-housed										
Oblique	Bill pointing downwards	lg	Small group	81	32	19	43	1.5	306	Typical of gulls <6 weeks
	Upright-like (neck vertical, bill horizontal)	lh	Small group	78	27	($< 10\%$)		3.6	306	Frequently in gulls of 4-10 weeks
	Body not tilting upwards but horizontally	li	Small group	(100%)		($< 5\%$)		($< 5\%$)		$> 10\%$ in gulls < 10 weeks
	Body extremely tilting upwards, neck vertical	lk	Common gull	(100%)		Often		Seldom		Dominant in social hierarchy
Forward	Neck position between oblique and forward	ll	Small group	93	14	Dead		5	100	Typical for young of 6-10 weeks
	Neck position between oblique and forward	ll	Small group	100	19	71	45	5	100	
	Neck not extended	lm	Common gull	(100%)		(100%)		20	179	Resembles incomplete forward
	Neck not extended	lm	Common gull	100	25	24	45	20	179	

Choking	Extreme turning movements to each side	1o	Isolation	?	?	83	47	3	202	Pecked itself in own carpal joints
Long-call	Strongly resembling mew-calls	2i,j	Small group	100	27	($<10\%$)		Never		
	Strongly resembling choking-vocalization	2k,l	Small group	0.25*	43	Mostly normal		0.78	50	Long-call develops from choking-call
	One long-note only	—	Common gull	1†	25	1.8	62	2.8	70	Fearful
After birds were re-housed	With head-flagging and one wing extended	1j	Isolation	69	26	25	67	5	302	
Oblique	Tail spread	—	Isolation	Fragmentary		82	34	($<5\%$)		
	During the posture, standing on top of feet	—	Isolation	Fragmentary		(100%)		Dead		
Choking	Incomplete posture, but with head-movements	1n	Isolation	100	11	?	?	3	202	
	Both wings almost completely extended	1p	Isolation	88	16	65	40	7	100	Fearful
Upright	Erratic with rapid head-flagging	—	Small group	(100%)		Never		Never		
Long-call	Notes as in landing- and choking-vocalization	2m,n	Little gull	(100%)		23	61	Never		Long call develops from choking-call

N is the number of postures from which the percentage of abnormal displays was calculated. Data in parentheses are estimated.

*Duration of longest note.

†Number of long-calls in the note.

Table III. Number of normal, deviating or fragmentary oblique postures that were accompanied by normal, hoarse or high pitched long-calls

Type of long-call	Type of posture		
	Normal	Deviating	Fragmentary
Normal	27	5	2
Hoarse	0	0	15
High	1	0	2

begging display in interactions with the animal caretakers (Fig. 2c, d). These were rather dissimilar to begging calls of birds reared in a large group (Fig. 2a, b).

Although normal in duration and sequence of notes and intervals, almost all long-calls accompanying fragmentary oblique display were abnormal in pitch. They sounded either very hoarse, or abnormally high. This was not the case for long-calls of deviating or normal obliques (Table III). High-pitched long-calls are typical for black-headed gulls younger than 7 months, and hoarse ones for birds of 6–10 months. Indeed the sonagram of a hoarse long-call given by a bird of 15 months reared in isolation is almost indistinguishable from a hoarse long-call given by a normally reared bird at the age of 6 months (Fig. 2g, h). Thus, hoarse or high sounding long-calls can be interpreted as the expression of a retardation in development of the display. This is in line with the finding that these calls are typical of fragmentary display, because the latter is also similar in form to incomplete display, which is typical of young gulls.

Testosterone and Display Development

The production of testosterone, as measured indirectly on the basis of the development of the brown mask, correlated positively and significantly with the frequency of oblique display in the adult black-headed gulls housed together in a large aviary during early spring (11 h observation time, Fig. 4a; $r_s = 0.56$, $N = 15$, $P < 0.05$). Such a correlation was also present in the juvenile gulls during late spring (10 h observation time; Fig. 4b; $r_s = 0.72$, $N = 11$, $P < 0.05$) and in the group of isolated birds (at least 10 h observation time; Fig. 4c; $r_s = 0.76$, $N = 14$, $P < 0.05$).

These results indicate that in adult as well as in juvenile gulls the production of testosterone is

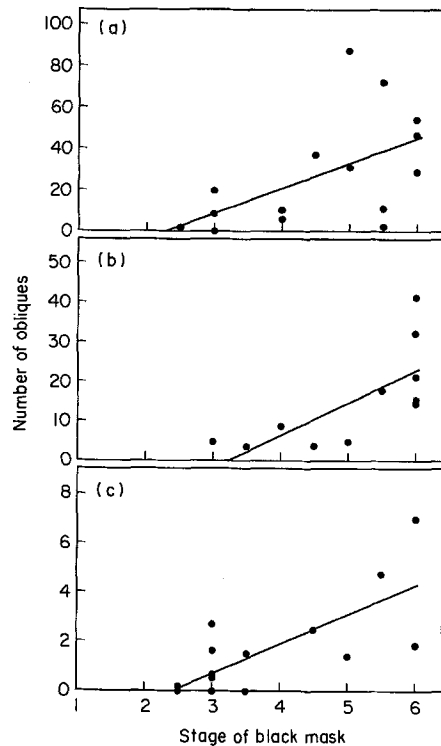


Figure 4. The frequency per h of oblique postures of individual gulls in relation to the stage of development of the black mask. (a) Adult gulls during early spring (March–April). (b) Juveniles of about 10 months in late spring (May–June). (c) Isolated birds of about 10 months in late spring (May–June).

related to the performance of display behaviour. I therefore analysed the relation between the development of the brown mask and the development of the form of the displays. Behavioural and mask scores were obtained for the birds that were reared in isolation from early on or in small groups, including the three birds that were reared in small groups of another species of the same age. There was a clear relation between form of display and the scores of the brown mask (Fig. 5; one-way ANOVA $F_3 = 6.86$, $P = 0.001$). Birds showing no or fragmentary display had less well developed masks than birds performing normal or deviating display. This indicates a relationship between testosterone and development of the form of the display.

A two-way analysis of variance revealed no significant effect of sex ($F_1 = 0.06$, $P = 0.79$), but a strong effect of rearing condition ($F_2 = 5.78$, $P = 0.006$) on the development of the mask (Fig. 6). The larger the group in which the birds were reared,

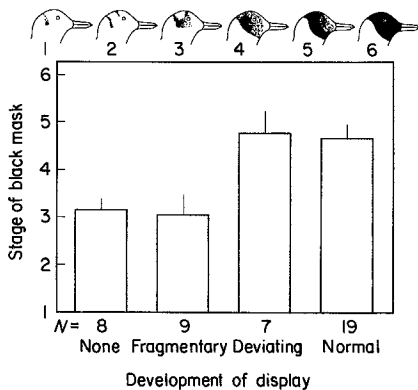


Figure 5. Mean (+SE) stage of development of the black mask in late spring, for four categories of birds, according to their development of display. Both scores were obtained in the original rearing conditions (in isolation or in small groups from early on) just before the birds were re-housed. For definitions see text.

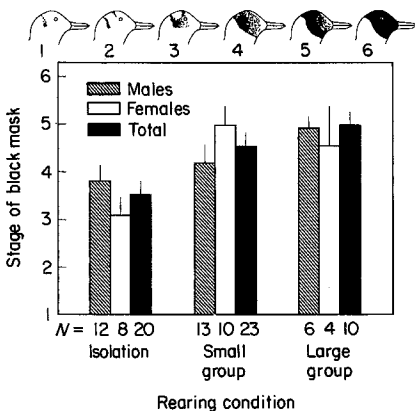


Figure 6. Mean (+SE) stage of development of black mask in late spring for three types of rearing conditions.

the further its development. This suggests an influence of social interactions on the production of testosterone.

DISCUSSION

The species-specific form of the displays of the black-headed gull gradually emerges in normal ontogeny, via incomplete motor patterns, to the complete adult one. Young black-headed gulls perform these incomplete displays almost exclusively in social interactions, suggesting that social

experience influences the development of displays. This suggestion was tested in the present study.

A high proportion of birds reared in small groups or in isolation showed in the adult stage either no display at all or fragmentary display (Table I). The latter were in form similar to the incomplete forms of display typical of young gulls, and were almost always accompanied by high pitched or hoarse long-calls, also typical of young gulls (Table III). Furthermore, none of these birds showed the complete adult form of display immediately when placed in a large group of conspecifics at approximately 10–12 months (Fig. 3). Moreover, some of the birds reared in small groups developed stereotyped deviations in the form of their display and this seems to be the first report with quantitative evidence for this phenomenon.

Imitation

One possible explanation for the occurrence of these abnormalities is the influence of imitation. Young gulls might have the development of the display retarded, or develop deviating forms of display if a model to copy is absent, or they might copy abnormal postures and calls from other birds only, if these are the only models present. Neither of these suggestions is supported by the data. Almost half of the gulls, reared in visual isolation from early on, were able to develop normal display and did not develop consistent deviations of the normal adult form (Table I). One could argue, however, that imitation, although not indispensable for normal development of display, could still be of some importance, because 60% of the isolated birds did not develop normal display. If so, one should expect that birds, when provided with deviating models to copy, develop deviating displays. This was not the case. Black-headed gull chicks, reared individually with other gull species, did not copy elements of display of these related species into their own display. Furthermore, the same deviation in form never occurred twice in the same small group of birds. Therefore, imitation is unlikely to be important for the development of display of black-headed gulls. This is not really surprising since imitation in animals that cannot see their own motor output is complicated because these animals must compare the model with the result of their own performance on the basis of different modes of information (in this case visual input with proprioceptive information).

Form Deviations and Social Reactions

An explanation for the occurrence of stereotyped deviations in the form of display might be that young birds shape their display on the basis of the response of other birds to their postures or calls. In this way deviations could be due to abnormal social interactions. This is suggested by the finding that stereotyped abnormalities in oblique display occurred only in the small groups, where birds could interact with each other, and not in isolated birds. Moreover, isolated birds could interact socially only with their human caretakers, to whom they performed begging displays, and the only abnormalities that were found in the display of these birds indeed occurred in this begging behaviour (Fig. 2a–d). It seems very likely that the social interactions of the isolates with their caretakers, and those occurring in the small groups, were not normal with respect to the behaviour of the reactor to the display performed by the actor. For example, birds reared in small groups had a clear social hierarchy, which was lacking in the large groups. This might have led to differences in the kind of agonistic interactions within large and small groups. Whereas birds in large groups must signal their tendency to attack clearly by means of display, for each agonistic interaction, birds in small groups may understand each other's tendencies more easily, as they have better knowledge of each individual bird's characteristics and social status. This might imply that in the small groups no pressure was present to show complete display, which is more often followed by subsequent attack than incomplete display (Groothuis 1989b). This would explain why some of the elements of deviations in form present in small groups were similar to those characteristics for incomplete display. It may well be that in some birds, reared in small groups, the form of display did not develop further because incomplete forms were sufficiently effective for communication within these groups. This implies of course that young gulls are able to distinguish between different alternatives of a display, and react consistently to each of these. That this may be the case is indicated by the following data. The probability of subsequent attack after an oblique posture of the bird performing the attack is highest when the bill points upwards in this posture, and lowest when the bill points downwards (Groothuis 1989b). Opponents seemed to anticipate these differences in attack probabilities after

display: they withdrew in 68% of the cases when the opponent performed a bill-up oblique ($N=289$), in 57% after a bill-horizontal oblique ($N=499$) and in 33% after a bill-down oblique ($N=75$). As one of the anonymous referees of this paper suggested, the idea that deviations in form are caused by the familiarity of the birds in the small groups could be tested by rearing birds in small groups in which the members are frequently replaced by new birds.

In conclusion, young gulls might learn to use the most effective alternative of a display, and these alternatives would then become stereotyped elements in their behaviour. A role of operant conditioning in the applications of displays has been suggested by several authors to explain shifts in contexts of postures during ontogeny (Kruijt 1964; Feekes 1972; Groothuis 1989b; Groothuis & Meeuwissen, in press). I suggest that this process also involves the development of the form of displays. An influence of operant conditioning has been suggested by Radesater (1974) for the development of the orientation component in the meeting ceremony in goslings, *Branta canadensis* and *Anser anser*. Furthermore, in cowbirds, *Molothrus ater*, performance of display by the female depends on the type of song produced by the male, and this female behaviour in turn affects the type of song males will develop (West & King 1988).

It may seem puzzling that some birds, reared in isolation, were able to develop normal adult display, despite the lack of reactions of conspecifics to their display. This seems to conflict with the idea that learning is important. Two explanations are possible.

(1) The form of display behaviour can develop along two alternative pathways, each resulting in the same species-specific form of display. Gulls reared normally in large groups might shape their display primarily on the basis of reactions of conspecifics, while isolated birds rely on another sort of information, from which the species-specific form of display can be extracted, possibly via proprioceptive feedback.

(2) Normally reared gulls as well as gulls reared in isolation might develop display independently of the learning process in question. However, development of display is open to influences of learning at certain stages. Only abnormal social interactions may then result in a deformation of the development of form e.g. when birds are reared in abnormally small groups.

Testosterone

The stage of development of the brown mask, taken as an indirect measure of testosterone production in the gulls, correlated positively with frequency and, more interestingly, with completeness in form of the displays (Figs 4 and 5). The difference in mask development between birds showing fragmentary postures and those performing deviating display is worth stressing. It justifies the distinction, made between the two categories of display, which might be looked upon as somewhat arbitrary or artificial.

The effect of testosterone on the development of the form of displays has rarely been studied. Several authors have reported precocious behaviour in young birds, treated with testosterone. Although detailed analysis of the form of display postures is lacking, there is some evidence that exogenously administered testosterone in young birds accelerates the emergence of adult display postures (Schein & Hale 1959; Andrew 1963; Kruijt 1964). Such an influence of testosterone on the completeness of the display in young animals raises the possibility that the potential for performing complete display is already present in the young gull, waiting for the right internal state, e.g. a high level of testosterone, to come about. This might imply that the performance of incomplete motor patterns is not necessary for the development of the complete ones. The temporary occurrence of the former may just be an inevitable epiphenomenon owing to a temporarily low level of testosterone. Experiments aimed at testing this idea are reported in another paper (Groothuis & Meeuwissen, in press).

The results also indicate that the more deprived of social interactions a young bird is, the more its production of testosterone is retarded (Fig. 6). Indeed, there is increasing evidence that the presence or behaviour of conspecifics can stimulate the production of testosterone (e.g. Silverman 1978; Cheng 1979; O'Connell et al. 1981; Hannes & Franck 1983; Delville et al. 1984; Wingfield 1984). Thus, it may be that, in the field, social interactions, and in particular aggressive interactions on the territory, stimulate the production of testosterone, leading in turn to the emergence of complete display.

Form Fixation

The idea that complete display, once developed during ontogeny, becomes fixed in form is

suggested by the following. (1) Adult gulls show stereotyped display, somewhat different from and less variable in form than the display of young gulls (Groothuis 1989a). (2) Normal oblique display and pronounced stereotyped deviating obliques, once developed, changed less often in form during the first weeks after re-housing than fragmentary display (Fig. 3). (3) Even after more than 1 year following re-housing the deviations were still performed regularly (Fig. 3). (4) Complete display, once developed by birds reared in large groups, was relatively resistant to change after subsequent isolation (Table I).

Fixation of form fits the suggestion that gull displays, once the form has developed under the influence of motivational factors for aggression and fear, become partly independent of these internal factors in older gulls. These may then be interpreted as subroutines applicable in several behavioural 'programs' (Groothuis 1989b).

Fixation of form might be the result of repeated performance of that motor pattern, which is supported by the observation that stereotyped deviating and normal display were performed much more frequently than fragmentary display before re-housing. However, this relation between form and frequency of the oblique might have been caused by testosterone. This raises the possibility that testosterone is involved in the process of fixation of form, either directly or indirectly via its effect on repeated performance. Further study is needed here.

Fixation of the form of deviating display was not absolute: almost all birds performed normal display after more than 1 year after re-housing. It is interesting to note, however, that most of the deviations in form could still be seen and heard when the bird was involved in highly aggressive interactions, whereas normally reared gulls use the same displays both in territorial disputes and in encounters with their own partner or chicks. This finding can be explained by two hypotheses.

(1) The occurrence of the deviations might be context-specific. All deviations were developed in agonistic interactions with conspecifics. As a consequence they are used only in such interactions, and not in interactions with the partner or with the bird's own offspring. Such interactions increase in frequency in birds more than 1 year old, which might explain the decrease in frequency of the deviating display.

(2) The bird might fall back on its old deviating subroutine when under stress, when it has to decide

very quickly what to do. Fentress (e.g. in Fentress & Mcleod 1987) found an interesting parallel in the return of old locomotion patterns in mice, *Mus domesticus*, and in a wolf, *Canis lupus*, when these were frightened and suggested that in such situations the animal performs already well established motor patterns, without evaluating peripheral input.

In summary, social interactions stimulate the production of testosterone in the young gull, which in turn may stimulate the development of complete display, which then becomes fixed in form. Imitation does not play a role in the development in form of the displays, but abnormal social reactions may induce stereotyped deviations in this form.

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